

TWO PHYSIOLOGICAL CONSIDERATIONS IN BIRD MIGRATION

BY W. B. YAPP

THE crossing of large expanses of sea by migrant birds has been known from time immemorial, and journeys of several hundred miles, such as those over the Mediterranean, over the North Sea from Europe to Great Britain, and over the Caribbean Sea, are commonplace. More recently it has become generally admitted that even the Atlantic is crossed quite often, even if not regularly. The evidence for Atlantic crossings from west to east has been reviewed by Alexander and Fitter (1955) and since their paper was published, the magazine *British Birds* has contained five new records of North American birds in Great Britain. The navigation which enables long sea crossings to be made, and the muscular and respiratory physiology which permits long flights to be sustained, are obviously of great interest. There is very little experimental evidence on either of these matters, and my purpose in this paper is to try to apply what little we do know, necessarily in a theoretical way, to the problem.

Williamson (1952 and 1954) has shown from a study of the weather maps that the most marked migration into Great Britain from northern Europe occurs in meteorological conditions which produce a steady east wind, and that the notable invasions of American birds occur with west winds. From these observations he has drawn the conclusion that, under conditions of strong wind over the sea, birds abandon their standard direction and fly downwind, so that they are brought more quickly to land. Clearly a strong wind, especially a cross wind, must have great effects on migrating birds, but for us to be able to assume that this particular type of reaction to cross winds always or generally occurs, we must be able to show, following current evolutionary theory, that it has such advantages over all other types of reaction that its production by natural selection is probable. The possibilities have never, so far as I know, been fully considered.

In the discussion which follows I use terms in the sense which they have in dynamics and air navigation. "Speed" is rate of change of position, that is, distance traveled per unit of time; "velocity" is speed in a particular direction, so that it is a vector; "course" is the direction in which the bird propels itself through the air; "track" is the line over the land which it follows as a result of its flight and of the wind, that is the resultant of its own velocity and that of the wind.

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POSSIBLE MEANS OF ORIENTATION IN OVERSEAS FLIGHTS

A bird out of sight of land and subject to a cross wind may do one of four things.

1. If it can continue to orient itself, it may continue flying in its standard direction, that is, on the course which has been laid down for the species in the past, presumably by natural selection. In daylight it determines this by some navigational clues which may include landmarks and the sun; at night, or at least on a dark night in latitudes and seasons where the direction of the sun below the horizon cannot be seen, it would need other means of orientation, but what these may be we do not know. If it does continue to fly in this way, the velocity of the wind must be added to the bird's velocity through the air, and if we know both of these we can find its track by the vector triangle method. To take a simple example, a bird which started to cross the Skaggerak at the south of Norway on a southerly course (180°) and encountered an east wind (90°) with the same speed as its own, would travel on a track of 225° and so arrive on the Yorkshire coast instead of in Denmark. Following the normal navigational usage it is to this type of displacement, and to this only, that the term "drift" should be applied.

2. The bird might, as Williamson suggests, recognize from the appearance of the sea the direction of the wind, abandon its standard direction, and reorient itself so as to fly downwind. I am informed that wind-lanes, which would seem to be the most likely clue by which the bird could determine the direction of the wind when out of sight of land, are only formed at speeds above Beaufort Force 4 (minimum speed 13 m.p.h.). The direction of movement of waves is an unreliable guide, since it may persist long after the wind has died down.

3. It would seem, however, that if the bird could tell the direction of the wind it might also be able to determine the relation of this to its own standard direction, and so be able to maintain the latter approximately by flying at the necessary angle to the wind. This would be comparable to normal air navigation, in which the course of the aircraft is calculated so that the vector triangle of the course plus the wind gives the required track.

4. If it had no navigational clues, and were unable to determine either its standard direction or that of the wind, the bird might continue to fly in what, to use anthropomorphic language, appeared to it to be the direction in which it started. I know of no experiments on this sort of blind flying, but for human beings walking, swimming and driving an automobile, the result of trying to keep a straight course with the eyes shut is in fact a large open curve, which approximates to a circle, and it is likely that the same would be true of a bird in flight. A bird doing this would still be

subject to drift. If the radius of the curve were large, the resultant track would be approximately the same as in 1 (derived from the bird's velocity and that of the wind). If the radius of the curve were relatively small, the track would be effectively that of the wind. The point of arrival on land would be the same as in 2 (changing course to fly downwind); the bird would, however, take longer to get there, for while in 2 its ground speed is the sum of that of the wind and its own air speed, in 4 it is that of the wind alone, since it spends as much time flying against the wind as with it. The same result would be given if the bird frequently changed its course. If the radius of the curve were of the same order of magnitude as the length of the sea crossing, the track of the bird would be effectively random.

Of these possibilities, 4 would clearly be disadvantageous and it would seem that a moderate radius of the curve in which the bird flies would be the worst. 1, 2 and 3, if the wind were in any degree a following wind, would all take the bird across the sea, but the points of arrival would be different. If the arrival coast were straight and ran at right angles to the bird's standard direction, the shortest crossing in terms of time would be made by 1 and the longest by 2, but if the coast were irregular and had bays and promontories, either 1 or 2 or 3 might bring the bird more quickly to land, according to the particular configuration of the land and the velocity of the wind. Condition 2 is likely usually to take longer than 3 and would only not do so if a high-speed wind happened to take the bird to a promontory which jutted far out from the coast. With so much variation it seems unlikely that natural selection could in any way discriminate among these three different types of flight. If 1 (maintenance of standard direction) is ruled out as improbable, it still remains true that 2 (flying downwind) would seldom be more advantageous than 3 (determining course from wind direction). Only if it were consistently so would Williamson's hypothesis of its choice by natural selection be possible. Since 4 (attempting to maintain a straight course without clues), though the worst of the four reactions, might be expected to lead to a large number of successful crossings and demands no special abilities in the bird, it is the one which for the present, on the principle of economy of hypothesis, ought to be accepted.

SOME ENERGY RELATIONS OF OVERSEAS FLIGHTS

At the end of a long sea crossing migrant birds are often exhausted, and it would be interesting to know from what sort of fatigue they are suffering and how near to every possible physiological limit they have gone. Williamson (1952) has reported that a number of birds weighed as they arrived at Fair Isle, off the east coast of Scotland, were lighter than the same species at the same time of year trapped at Lista in Norway. While it is interesting

that a loss in weight is probably demonstrable by weighing small numbers of trapped birds (though measuring such a variable quantity as the mass of a bird to four significant figures represents misplaced zeal), it would be more interesting still to know in what the loss consists and how near it goes in an average sea crossing to the theoretical and practical limit. The first of these, on which the second depends, could be determined only by chemical analyses of the bodies of migrating birds before and after their journey, but the following calculation, though approximate, may suggest the order of magnitude of the loss which might be expected.

There are several types of flapping flight, but it seems that in general in fast and moderately fast flight the up-stroke is passive, and this is true also of small birds in slow flight (see Brown, 1953, and the same author reported anonymously in *Nature*, 1955). Such flight means that the bird must fall during the up-stroke and rise again during the down-stroke, and it is easy to calculate the energy expended by the bird in maintaining itself in the air in this way. If any lift is contributed by the upstroke of the wings, as happens in larger birds in slow flight, there is a greater mechanical efficiency and less energy is needed.

Let the weight of the bird be x gms. weight, and let there be n wing beats per second. If downstroke and upstroke are of equal duration (as Brown, 1953, has shown to be true of the gull in fast flight) between two successive downstrokes the bird falls a distance

$$d = \frac{1}{2} \times \frac{g}{4n^2} \text{ cms.}$$

The work done during the upstroke to raise it again, is

$$f \times d = \frac{xg^2}{8n^2} \text{ ergs,}$$

and work done per second is

$$\frac{xg^2}{8n} \text{ ergs.}$$

The work done per hour is

$$\frac{3600xg^2}{4.2 \times 10^7 \times 8n} \text{ cal.}$$

This energy might be provided by the combustion of carbohydrate (probably chiefly glycogen) or of fat. Different carbohydrates have slightly different energy values (Benedict and Fox, 1925), but an average value seems to be 4100 calories per gram. I have not been able to find any figures for the efficiency of avian muscle, but the maximum for frog muscle is about 20 per cent and that for human muscle 22 per cent (Hill, 1939). In view

of the closeness of these two figures for rather widely separated vertebrates, it is unlikely that bird muscle is greatly different. The efficiency depends on the speed of contraction of the muscle, and falls off fairly rapidly on each side of the optimum. It is unlikely that the bird can maintain the optimum steadily for very long periods, however much it may approximate to a steady rate of wing-beat. There is also a loss of energy because the aerodynamic efficiency of the wing-stroke is less than 100 per cent, although it seems impossible to calculate this (Brown, 1955). Further, some energy is needed to overcome air-resistance, although at speeds of up to about 30 m.p.h. this is likely to be small in comparison with that needed to maintain the bird in the air. It would seem to be safe, in trying to calculate the maximum amount of food material used in flight, to take all these points into account by giving the wing an over-all efficiency of half its maximum, or 10 per cent. The work done per hour therefore represents the consumption of

$$\frac{3600xg^2}{4.2 \times 10^7 \times 410 \times 8n} \text{ gms. carbohydrate.}$$

Meinertzhagen (1955) has recently published figures for the rate of wing-beat of many species. For small and medium sized birds 5 beats per second seems to be a fair average value to take for cruising speed. Meinertzhagen contends that birds on migration fly much faster than usual, so that a value of $n = 10$ would not be far wrong, but if we take the lower value we shall get a maximum consumption of the food stores.

If $n = 5$, the carbohydrate consumed = $0.00503x$ gms., that is, 0.5 per cent of the mass of the bird is used up per hour. If the chief source of energy is fat, as has been claimed for the House Sparrow (*Passer domesticus*) by Kendeigh (1944), and as appears likely from the well-known deposition of fat prior to migration (see, for instance, Odum and Perkinson, 1951), the loss will be less. One gram of fat produces 9,500 cal. (Benedict and Fox, 1925), so that the work done per hour represents

$$\frac{3600xg^2}{4.2 \times 10^7 \times 950 \times 8n} \text{ gms. fat.}$$

If $n = 5$ as before, this = $0.00217x$ gms., that is, 0.2 per cent of the mass of the bird is used up per hour.

Energy is also required for the maintenance of body temperature. Kendeigh (1944) has shown that in the House Sparrow this is, at 10°C external temperature, approximately $35x$ calories per hour, where x as before is the body weight in grams, which represents $0.0085x$ gm. of carbohydrate or $0.0037x$ gm. of fat. A small bird therefore uses its reserves nearly twice as rapidly to maintain its temperature as for flight. Since our figures for energy consumption have been maxima throughout, and since the air tempera-

ture will often be less than 10°C , this factor will almost certainly be exceeded as a rule. Most of the waste energy of the muscular contraction (we have taken this to be between 80 and 90 per cent) will be available for maintaining the temperature, and the total loss of reserve material appears to be of the order of 1 per cent of body weight per hour if it is carbohydrate, or 0.4 per cent per hour if it is fat.

If a bird crosses the North Sea from the Skaggerak to Fair Isle at an air speed of 30 m.p.h. with a following wind of 20 m.p.h., its ground speed will be 50 m.p.h., and its flight will take approximately six hours, so that it will lose some 6 per cent or 2.4 per cent of its mass according to whether it uses carbohydrate or fat. Williamson's experimental figures suggest that the loss is, in fact, more like 10 per cent. There are two possible sources of this extra loss. The bird may defecate during its crossing, and if we assume that it starts its flight immediately after feeding it certainly will do so, and it will lose water from the lungs and air sacs. Kendeigh found the total loss of moisture from his House Sparrows to be $0.005x$ gms. per hour for birds at rest at 10°C external temperature. This is approximately one and a half times the loss by combustion of fat under the same conditions, and, as in the combustion of fat the oxygen taken in very nearly balances the carbon dioxide given out, means that the bird is losing stored water over and above the metabolic water which represents the loss of oxidized material. Dawson (1954), who worked on the Brown and Abert towhees (*Pipilo fuscus* and *P. aberti*) found that at 39.5°C the birds drank more water than, as shown in a parallel experiment, they lost by evaporation. In flight, the evaporation of water will presumably be greater than when the bird is at rest, but by how much we do not know. If it rose to the level which both Kendeigh and Dawson found for birds at rest at an air temperature of 40°C , the loss for a six-hour flight would be about 10 per cent. Williamson's figures therefore appear to be remarkably close to the best theoretical forecast that one can make. (The evaporation of the water of course needs energy; for a loss of 0.015 gm. per hour it would be 8.6 cal. per hour. There is no means of telling how much of this has already been included in Kendeigh's figure of $35x$ cal. per hour for heat maintenance, but some of it will have been so included, and the addition of the rest does not greatly affect the magnitude of our result.)

If my interpretation is correct, the limits of a long flight may well be set by thirst rather than by hunger. Williamson (1954) has contended that on such flights, as for example in the west to east crossings of the Atlantic, it is a positive disadvantage for a bird to rest on a ship. The basis of this contention is that the bird will, if it flies on with a following wind, just about have exhausted its food reserves when it lands, so that anything which delays

landfall is likely to be fatal unless food can be picked up during the rest. Even if for most of the species of birds concerned little food is likely to be available on board ship, water, in the form of dew or rain, will often be present, and a rest may therefore be very helpful to a bird suffering from thirst.

Odum and Perkinson (1951) have shown that the body-weight of White-throated Sparrows (*Zonotrichia albicollis*) is about 20 per cent less in October and November (after migration) than it is in April and May (before migration) and that almost all this loss is of fat. These birds have not made a long sea-crossing and presumably are not near exhaustion, so that larger losses could be borne before death would occur. We do not know how rapidly the fat can be metabolized. Wigglesworth (1949) found that when fruit flies (*Drosophila*) were flown to exhaustion, they could fly again, either after a rest with no food, or almost immediately after being given soluble carbohydrates. The period of flight following a rest (but before exhaustion again set in) was longer the longer the rest; after an hour it was about one-sixtieth of the duration of the previous flight. These observations agreed with analyses of the body composition which showed that during flight fat did not disappear. Presumably it was converted to carbohydrate, and so made available during the rest.

It is possible that the chemistry of bird flight might be similar, although it would be dangerous to argue from insects to birds without experiment. If it were, a rest on a ship would allow an exhausted migrant to change stored fat into carbohydrate, and so allow it to recover and fly further, quite apart from the provision of food or water. The muscular physiology of birds, although little is known about it, is unlikely to differ in principle from that of frogs and mammals. Here there are several sources of fatigue: chemical substances other than carbohydrate may fail, there may be too great an accumulation of lactic acid, the nerve-muscle junction may cease to act, or the central nervous coordination may be upset. Fatigue due to some of these may be abolished merely by rest, as happens especially in human sleep. To determine the chief cause of the fatigue of arriving migrants would need experimental work, but much might be learned by observation of the conditions under which they recover. Until more is known it cannot be assumed that a rest on a ship is harmful.

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